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Observations on the Range and Natural History of *Monadenia setosa* (Gastropoda: Pulmonata) in the Klamath Mountains, California, and the Taxonomy of Some Related Species

by

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Abstract. *Monadenia* (*Monadenia*) *setosa* occurs mainly in riparian corridors with dense deciduous understory in Trinity County, California, U.S.A. Eastward, *Monadenia* (*Shastelix*) *churchi,* which within the range of *M. setosa* is restricted to open hillside habitats, occupies streamside habitats. On the north and west, *M. setosa* is replaced by *Monadenia* (*Monadenia*) *fidelis,* with a narrow zone of intergradation. One population, with a density of 0.11 snail/m^2, was monitored over an annual cycle. Capture of marked individuals departed significantly from randomness. Widely varying population estimates reflected irregular snail activity patterns. Reproductive maturity apparently occurs at different seasons of the year; early growth is probably rapid, slowing as maturity is approached. Feeding occurs on the ground and on the trunks of trees with smooth bark. Both adults and juveniles occur on the ground and also climb vertical surfaces. Beetle and possible rodent predation occur; the latter may often be unsuccessful. Limited home ranges, probably related to available shelter, may exist. *Monadenia* (*Monadenia*) *callipeplus* of the Scott River drainage represents a parallel development of a bristly shell surface. *Monadenia* (*Monadenia*) *scottiana* is elevated from a subspecies of *M. fidelis* to species rank. *Monadenia chaceana* is restored to species rank and assigned to the subgenus *Monadenia* s.s.

INTRODUCTION

LITTLE PUBLISHED INFORMATION exists on the ecology or life history of snails of the New World helicacean family Helminthoglyptidae. The most extensive contributions are those by VAN DER LAAN (1971, 1975a, b, 1980) on what he called *Helminthoglypta arrosa* (actually the distinct species *H. stiversiana* [Cooper, 1875]; ROTH, 1982) and the accounts of a 1978 field study of *Monadenia* (*Monadenia*) *setosa* Talmadge, 1952, in the Shasta-Trinity National Forest, California, U.S.A., for the U.S. Forest Service (ROTH, 1978; ROTH & ENG, 1980). In contrast to *H. stiversiana,* which occurs in large numbers in a relatively uniform habitat (coastal *Lupinus* scrub), *M. setosa* is a species of cryptic habits, occurring in low densities in a structurally complex forest habitat.

The 1978 study of *Monadenia setosa* included drainages that are tributary to the Trinity River from Italian Creek (secs. 14, 23, T. 5 N, R. 7 E, Humboldt Base and Meridian) to Manzanita Creek (secs. 32, 33, T. 34 N, R. 12 W, Mount Diablo Base and Meridian), all in Trinity County, California. *Monadenia setosa* was found living in the canyon of Swede Creek, and empty shells in the drain-

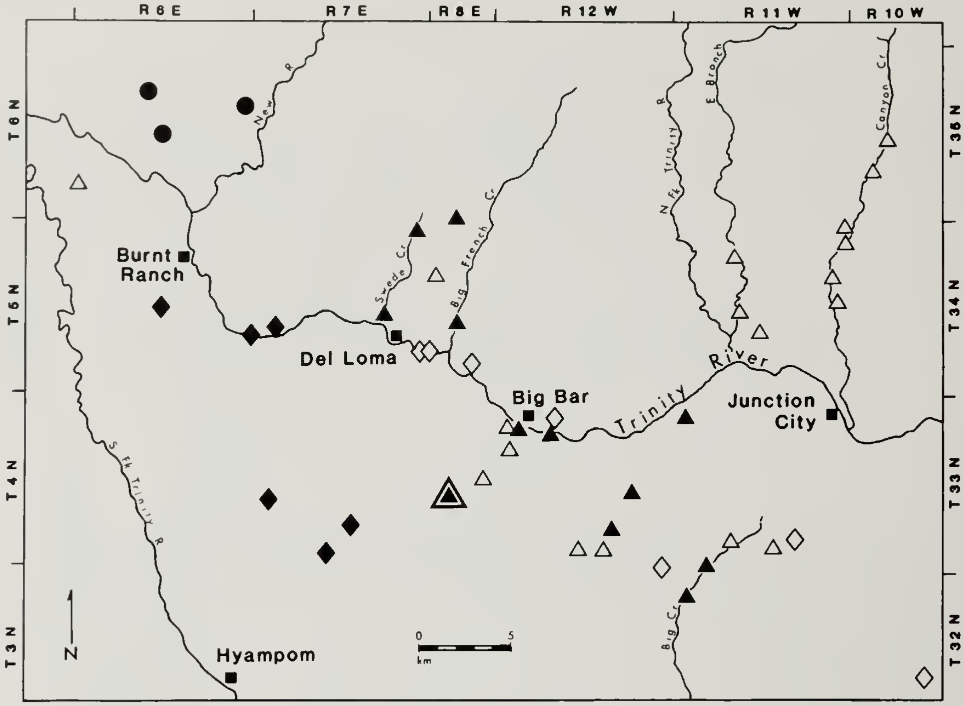


Figure 1

Location of sampling stations and distribution of *Monadenia* species. Solid triangles, *M. setosa*; solid circles, *M. fidelis*; solid diamonds, *M. fidelis*-*M. setosa* intergrades; open diamonds, *M. churchi*; open triangles, no *Monadenia* present. Large triangle, Bidden Creek monitoring site.

ages of Little Swede and Big French creeks. The finding of juvenile snails under loose bark of standing dead trunks of broadleaf trees, while adults were found on the ground, led to the suggestion that standing broadleaf deadwood, as a special juvenile habitat, might be a limiting resource. The species was reported to be restricted to riparian corridors with dense, mixed hardwood understory, either on canyon slopes or streamside benches. Only empty shells were found on the surface of talus slopes away from the watercourses; these shells were assumed to have been displaced from elsewhere. Drier slopes with an oak-madrone-douglas fir association supported a different assemblage of mollusks, without *M. setosa*. These findings were used in an interim management plan adopted in 1979 by the Shasta-Trinity National Forest (ROTH & ENG, 1980).

The present paper reports the results of additional field study of *Monadenia setosa* sponsored by the Forest Service in 1981–1982. The area of consideration was expanded to include the zone of Big French Creek identified as probable habitat in the interim management plan, regions of suitable habitat on the south side of the Trinity River and subsidiary drainages south to Hayfork Creek, and drainage divides north of Swede Creek and Big French Creek. This resulted in extending the known range of *M. setosa* to the north, east, and south (Figure 1).

One selected *Monadenia setosa* population was studied in the field at approximately 3-wk intervals over a complete annual cycle. The study included (1) an estimate of population size by mark-and-recapture technique, (2) size data for estimates of population age structure, individual life-span, and age at reproductive maturity, (3) observation of site selection by adults and juveniles to test the apparent dependence on standing deadwood suggested by the 1978 study, (4) records of individual movement and daily and seasonal activity patterns, (5) observations on feeding, and (6) an estimate of the possible effect of vegetational succession on *M. setosa* habitat.

Reproductive activity was watched for but was not observed, nor were egg clutches seen in the field.

Monadenia callipeplus Berry, 1940, was sampled at its type locality, Tompkins Creek near the Scott River, and dissected to determine whether *M. callipeplus* might be merely a remote occurrence of *M. setosa*. The reproductive systems of *M. callipeplus* and *M. scottiana* Berry, 1940, are illustrated herein and the taxonomic status of these species discussed.

The Office of Endangered Species of the U.S. Fish and Wildlife Service regards *Monadenia setosa* as a "candidate species" for Endangered or Threatened status (*Federal Register*, 49:21674, 22 May 1984). *Monadenia setosa* is officially listed as a rare species in Section 670.5, Title 14, California Administrative Code.

SETTING

The Klamath Mountains occupy a region between the Pacific Ocean and the southern end of the Cascade Range; on the southeast they are bordered by the Great Valley of California and on the southwest by the northern California Coast Ranges. They consist of old (early Paleozoic through Jurassic), complexly abutted rock suites and, to judge by the general absence of younger marine sediments, have included positive land area for much of Mesozoic and probably all of Cenozoic time (Davis *et al.,* 1978). The Klamath region is unique in terms of plant geography, having ". . . one of the most highly complex vegetation patterns in North America . . . . Into this area extend and meet in a complexly interdigitating pattern, various types of vegatation which form the prevailing climaxes of other areas. All western plant formations dominated by trees occur in the Klamath Region, as in no other area. Those forest formations that are of most highly mixed tree-stratum composition and are thought most to resemble Arcto-Tertiary forests in the West occur in this region—the redwood forests and mixed evergreen forests. Of these the mixed evergreen forest is the link between two major fractions of western forest vegetation—the coniferous forests, and the sclerophyll and oak-pine woodland grouping. The Klamath Region has also an exceedingly rich flora for its latitude; it is a center of floristic diversity and narrow endemism . . . , and many plant genera have maximum numbers of species in the West, including endemics, occurring there" (Whittaker, 1961:5–6).

In the area studied the prevailing climax is the Mixed Evergreen Forest of Munz & Keck (1959): mixed forests with two-level canopies of larger coniferous trees—douglas fir (*Pseudotsuga menziesii*) and yellow pine (*Pinus ponderosa*)—and smaller broadleaf-evergreen or sclerophyllous trees (*Lithocarpus densiflora, Arbutus menziesii, Castanopsis chrysophylla,* and *Quercus chrysolepis*). Deciduous trees (*Acer macrophyllum* and *A. circinatum, Cornus* sp., *Quercus kelloggii,* and others) are also present, mainly along watercourses. Whittaker (1961) observed that in relation to moisture the canopy changes from mesic stands in which the coniferous stratum is dense and deciduous trees may outnumber sclerophylls, through stands in which the conifers are scattered in open growth above a dense sclerophyll stratum, to more xeric stands in which both strata are open and pines (*P. ponderosa* for the most part) replace *Pseudotsuga* as the principal conifers. Particularly in some of the steeper canyons in the study area (for example, the canyon of Swede Creek described by Roth & Eng, 1980) the transition from riparian facies with dense deciduous understory to open stands is quite abrupt, or at least gradational over a few tens of meters, with individual understory species occupying rather well-defined zones parallel to streams.

On a regional scale, the density of conifers increases and that of sclerophylls decreases toward the more humid environments nearer the coast; *Pseudotsuga* becomes more prevalent and, finally, beyond the limits of the study area, there is gradation into the coastal *Sequoia* forest. Toward the drier interior, *Pseudotsuga* declines, the sclerophyll strata become more open, and the mixed evergreen forests grade into pine-oak foothill woodland (Whittaker, 1961). The effects of complex local topography, interacting with these regional trends, produce a mosaic of vegetational types, as readily seen on Forest Service timber-type maps.

DISTRIBUTION STUDY

Methods

The distribution of all land mollusks was investigated in an area roughly defined by Ripstein Campground, north of Junction City (on the NE), Hawkins Creek (NW), Hyampom (SW), and Hayfork Summit (SE), with additional study along Hayfork Creek as far south as Natural Bridge Picnic Area (Figure 1) (approximately 123°00′–123°30′W longitude by 40°37.5′–40°52.5′N latitude). The westernmost stations, on Hawkins Creek and Hennessy Ridge, are in Six Rivers National Forest and were searched to confirm the observation that *Monadenia setosa* does not extend this far west. More specific search, focusing only on the distribution of *Monadenia,* was also carried out, and additional findings by Forest Service personnel and W. B. Miller of the University of Arizona are included in the range report. All stations are in the watershed of the Trinity River and its tributary streams, including New River. Mollusks were located using standard field techniques: visual search in areas of likely looking cover, in brushpiles, around and under logs, in rock crevices and rockslides (down to the level where soil left no more crawl-space for mollusks), and so forth. Where field inspection showed minute shells to be present, leaf litter was collected and sifted in the laboratory for micromollusks. Reports on other species of mollusks beside *M. setosa,* molluscan faunal associations, and descriptions of new species are being presented elsewhere (Roth & Pressley, 1983, and in preparation; Roth, 1985a, b).

Field work was conducted from September 1980 to October 1981 with at least some sampling during every month of the year. Spring and autumn were the most productive times. Locations of sites yielding mollusks are listed by section, township, and range in the Appendix. Also included are sites surveyed from May to September 1978, in drainages that are tributary to the Trinity River from Italian Creek to Manzanita Creek (Roth, 1978). Localities were categorized as being either (*A*) within the zone of dense deciduous understory, or (*B*) in stands of open growth.

Results

Of the 38 general sampling stations occupied, 11 yielded *Monadenia setosa.* Figure 1 presents the species' distribution as shown by all material examined. This is a substantial extension of known range over the distribution shown by the 1978 study.

New marginal stations defining the range are Localities 2, 3, 4, 11, 12, 19, and 30 (see Appendix for locality descriptions). Only empty shells were found at the northernmost station, Loc. 2, but there is no reason to doubt that the species lives there. In addition to the stations cited, earlier in 1980 Forest Service personnel found *Monadenia setosa* in SE¼ sec. 6, T. 33 N, R. 11 W (near Eagle Creek); SE¼ sec. 22, T. 33 N, R. 12 W (drainage of Big Bar Creek); and perhaps also sec. 14, T. 33 N, R. 12 W (Big Bar Creek; specimen not seen by us).

Repeated search east of the Limestone Creek and Big Creek localities (Locs. 11, 12) yielded no *Monadenia setosa,* so this probably approximates the southeastern limit of its range. Negative results were also obtained north of the Trinity River along Canyon Creek, the North Fork of the Trinity, and Big French Creek north of Loc. 30, even in apparently suitable habitat. At many of the eastern localities, *M. setosa* is absent but *Monadenia churchi* Hanna & Smith, 1933, is present in ecologically analogous situations. A few kilometers south of Loc. 11, Big Creek flows through lightly forested foothills and debouches into Hayfork Valley, where the appropriate riparian habitat is lacking. Search along tributaries of Hayfork Creek, entering Hayfork Valley from the south, produced *M. churchi* but no *M. setosa.*

West of the localities cited, no typical *Monadenia setosa* have been found. The areas of Hawkins Creek, Hennessy Ridge, and New River yielded *Monadenia fidelis* (Gray, 1834). At Don Juan Creek, Cedar Flat, and McDonald Creek above Burnt Ranch occur *M. fidelis* with a partially matte base and light scattering of bristles on the shell. This may be a zone of past or present genetic exchange between *M. fidelis* and *M. setosa.* Further analysis is needed to show whether simple intergradation or secondary contact and hybridization are present; the narrowness of the zone and its apparent distinctness suggest the latter. Shells taken by Forest Service personnel at Clark Creek (sec. 19, T. 4 N, R. 7 E), Hyampom Creek (sec. 27, T. 4 N, R. 7 E), and a fork of Corral Creek (sec. 33, T. 4 N, R. 7 E) are of similar character and may represent a southern continuation of the hybrid zone.

Discussion

Except for Hayfork Valley on the south, the boundaries of the range of *Monadenia setosa* do not coincide with any obvious topographic or vegetational discontinuities. As noted above under "Setting," the region is gradational between humid coastal-subcoastal forest and the more arid interior. Geologically, all localities with typical *M. setosa* fall within a varied belt of Paleozoic and Triassic metamorphic rocks (see IRWIN, 1960:plate 1). Localities with *M. fidelis* or the suspected hybrids are on the chiefly granitic terrane of the Ironside Mountain batholith. To the east, the belt mapped as pre-Silurian (?) schists has yielded neither species. It is not clear how this underlying geology might affect the distribution of snail species.

Monadenia setosa lies on the eastern edge of the subgenus *Monadenia, sensu stricto* (compare map in ROTH, 1981: figure 1). East of the range of *M. setosa, Monadenia churchi,* which within the range of *M. setosa* is restricted to open stands and exposed slopes, comes to inhabit riparian corridors with deciduous understory. *Monadenia churchi* belongs to the inland subgenus *Shastelix* (ROTH, 1981:figure 1) and its range extends eastward around the head of the Sacramento Valley. It is undoubtedly more tolerant of xeric conditions than *M. setosa.* Up to a certain threshold (possibly having to do with temperature range) *M. setosa* may be competitively superior in riparian woodland situations and exclude *M. churchi* from this habitat. However, except for some work on the agonistic behavior of slugs (ROLLO & WELLINGTON, 1977, 1979), little is known about land mollusk interactions that could lead to competitive exclusion.

In terms of thermal parameters (mean annual temperature and mean annual range of temperature), the subgenera *Monadenia* s.s. and *Shastelix* show little overlap (ROTH, 1981:figure 18). (Note that on this graph of thermal ranges, Big Bar is the station defining the "continental" corner of the *Monadenia* s.s. polygon.) Evidence for the relationship between temperature and distribution in *Monadenia* is also discussed by ROTH (1981).

MONITORING STUDY

Methods

Following a preliminary reconnaissance in early September 1980, a 1044-m² study site was selected on the lower reaches of Bidden Creek in the SE¼ sec. 19, T. 4 N, R. 8 E (Humboldt Base and Meridian). This site presents a considerable variety of microhabitats within a riparian woodland facies and supports a substantial population of *Monadenia setosa.* The study site extends on either side of Bidden Creek, which here flows at a low gradient a few hundred meters from its confluence with Corral Creek. The site is bounded on the north by a steep bank and on the south by a low bank rising to a cleared and graded campsite. Outside the riparian corridor the vegetation is mixed evergreen forest with douglas fir, white fir, giant chinquapin, and canyon oak.

Major features of the site were mapped at a scale of 1: 100 with a Brunton compass and range finder (Figure 2a). Within the site the predominant trees are alders (*Alnus rhombifolia*), with douglas fir and black oak (*Quercus kelloggii*) less numerous. Standing deadwood, mostly alder, is present and there are logs and large branches on the ground. These remained virtually in place over the course of the study. Shrubs, mostly vine maple (*Acer circinatum*) with slim, multiple trunks, are also present.

Most of the area of the study site is gravelly stream terrace, well drained and covered with a layer of leaf-

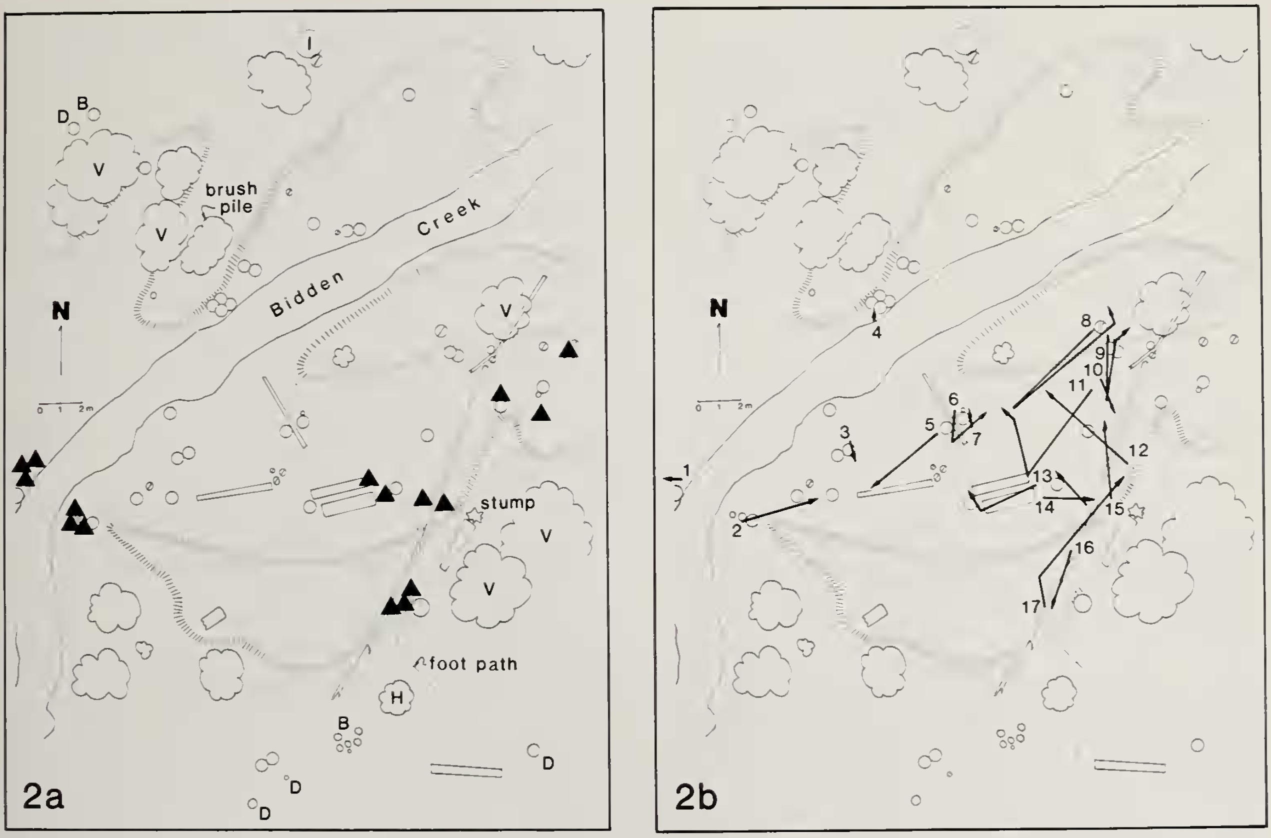


Figure 2

Map of monitoring site on Bidden Creek. Figure 2a. Distribution of snail captures (solid triangles) on a typical sampling occasion, 8 May 1981. B, black oak, *Quercus kelloggii*; D, douglas fir, *Pseudotsuga menziesii*; H, California hazel, *Corylus cornuta* var. *californica*; I, incense cedar, *Calocedrus decurrens*; V, vine maple, *Acer circinatum*; unlettered circles, alder, *Alnus rhombifolia*; slashed circles, standing dead trunks. Rectangular forms are logs and large branches on ground. Figure 2b. Locations of multiple captures during monitoring study; arrows connect successive captures of numbered snails.

mold—thus agreeing with preferred *Monadenia setosa* habitat as determined by Roth & Eng (1980). Water flowed over much of the area episodically during winter 1980–1981, but the site was not subjected to extreme flushing action. Hatched areas on the map outline 1–3 m high, downstream-trending piles of cobble- to small boulder-sized metavolcanic rocks, most with the rounded edges of stream cobbles. The piles are probably the result of past mining operations. Rocks in the top half-meter are loose, but the lower ones are more or less silted in; many crevices remain and provide mollusk shelter, especially for the big slug *Ariolimax columbianus* (Gould, 1851). The rock piles are moderately overgrown by shrubs, but most of the trees in the site grow on the unencumbered stream terrace.

A mark-release-recapture study was carried out with sampling at approximately 3-wk intervals beginning 24 October 1980. The site was searched systematically with flashlights in the first 2 h after dark. In order not to affect the sampling properties of the site, the search was made without disrupting rock piles or other potential shelter. Snails were individually tagged on the shell with numbers in India ink covered by a daub of clear nail polish. When necessary, the shell was dried first with a jet of compressed air. This tagging method does not appreciably alter the image of the shell and, thus, should not have affected the probability of recapture or predation. After marking, the snails were returned to their original site and orientation. Snails found sealed to the substrate were marked in place.

Altogether, 68 snails were captured and marked; 19 of these were recaptured at least once. For each capture the following were recorded: location, substratum, state of activity and orientation, shell diameter in mm, number of whorls (counted by the method of Pilsbry, 1939), whether adult (with reflected lip) or juvenile, and distance from nearest active neighbor. Capture sites were marked in the

Table 1

Data from mark-release-recapture study and parameters from Jolly's stochastic multiple-recapture analysis.

Day	Date	No. in sample	No. released	Proportion of recaptures	No. marked snails at risk[1]	Total population[1]
1	24 Oct 80	2	2	—	—	—
2	25 Oct 80	10	10	0	0	—
3	27 Apr 81	5	5	0	11.67	—
4	8 May 81	17	16	0.118	23.33	198.3
5	9 May 81	2	2	0	14.00	—
6	10 May 81	8	8	0.500	52.00	104.0
7	26 May 81	6	6	0.333	74.00	222.0
8	27 May 81	12	11	0.417	93.00	223.2
9	28 Jun 81	1	1	0	—	—
10	2 Oct 81	16	16	0.313	21.00	67.2
11	3 Oct 81	5	5	0.600	15.50	25.8
12	4 Oct 81	12	—	0.583	—	—

[1] Calculated by method of Jolly (1965).

field with aluminum nursery tags; on subsequent recapture, the horizontal distance from the last release was measured.

Population size was estimated by linear regression of the percentage of recaptures in a given session's sample versus the total number of snails marked. Extrapolating the regression equation to the 100% level gives an estimate of population size (Hadfield & Mountain, 1980). Jolly's stochastic multiple-recapture method (Jolly, 1965) gave problematic results probably influenced by snail activity and sheltering habits.

Capture records of 8–10 May 1981 and of 2–4 October 1981 were pooled to produce two estimates of shell-size frequency in the population. Size-frequency distribution was examined as an indicator of population age structure.

Results and Discussion

Population size: Linear regression analysis gives a population estimate of 112 snails. The equation is $y = 0.959x - 6.962$ with a correlation of $r = 0.760$. For the 1044-m^2 study site, this translates into a density of 0.11 snail/m^2. The regression method, assuming as it does a constant population size with no dilution (birth and immigration) or loss (death and emigration), provides a simple but mechanical estimate; it states, in effect, that if the calculated linear relationship were to hold good, then 112 snails would represent 100% of the population.

Table 1 presents the data of the mark-release-recapture study and population estimates based on Jolly's multiple-recapture method. No captures were made from November 1980 through March 1981 and July through September 1981, reflecting winter and summer inactivity periods. These dates are omitted from the analysis; the calculations are not affected. A much larger population is indicated in May than in October 1981, even though the number of captures remained similar. Either massive mortality or emigration between the spring and autumn sampling could have produced such results. However, the October samplings showed no other evidence of heavy mortality, such as empty shells. There were no scouring floods in this interval and extensive emigration seems improbable, given the apparent tendency for snails to occupy a limited home range over the course of a year (see below, "Substratum, location, and mobility"). Summer, with the onset of hot and dry conditions, is an unlikely time for snail dispersal to increase. Rollo & Wellington (1981) have demonstrated increased sheltering behavior by slugs at this time, and the summer drop in the number of active *Monadenia setosa* observed probably represents the same seasonal trend. Search during May, when fresh vegetation was extensive at the study site, may have been less efficient than in October, when the vegetation was sparse and beaten down; but marked and unmarked snails should not have been differentially affected.

A variance test for the randomness of recapture (Southwood, 1966:77) yielded a probability much less than 0.001. It seems likely that visual search without disruption of the substrate detects mostly active snails and that these do not represent a random sample of the population at large. The wide range of estimates for successive dates (8 May, 198 snails, versus 10 May, 104 snails; and 2 October, 67 snails, versus 3 October, 26 snails) further indicates the limitations of this method: it is implausible that the population should have decreased by 50% overnight.

The probability of a snail's being active on a given night may not be independent of its state of activity on the preceding night. If, for example, a foraging snail tends to feed to satiation on one night then retire to shelter for one or several days while digesting the meal, its probability of recapture during that period will be lowered. If, on the other hand, foraging is stimulated by a particular combination of microclimatic variables, and the key combination occurs at different times in different microhabitats within the study site, then foraging by individual snails (or "neighborhood groups" of snails) may be highly clumped in time. The first situation will tend to raise the population estimate (fewer recaptures on the second of two close sampling dates), and the second, conceivably, to lower it (more recaptures of the same snails).

The complexity of snail activity patterns tends to violate the assumption of equal catchability. Parr *et al.* (1968), Heatwole & Heatwole (1978), and Hadfield & Mountain (1980) reported similar problems in applying capture-recapture methods to snail populations. A program of greater sampling intensity might overcome the influence of irregular snail activity.

Growth and age: Pooled data on whorl number from 8–10 May 1981 and 2–4 October 1981 are presented in

Figure 3. "Adult" shells are defined as those with a reflected lip at the aperture. Formation of a reflected lip often, although not invariably, coincides with reproductive maturity in land snails. WILLIAMSON (1979) recorded that some *Cepaea hortensis* with reflected lips proved on dissection to have poorly developed genitalia while others had fully developed reproductive organs. *Theba pisana* may be reproductively mature while still in the phase of active shell growth (COWIE, 1984). However, in *Monadenia setosa* dissected by us, all those with a reflected lip, and none of those without, have had fully developed genitalia.

Once a reflected lip is formed, the shell does not increase in diameter or whorl number, so that shell size ceases to be an indicator of age. The tendency for individual *Monadenia setosa* to occupy a home range subjects each one to an individual regime of shell erosion and wear. Thus, periostracal wear, used by WILLIAMSON (1979) for *Cepaea,* is of doubtful use as an age indicator.

May and October distributions are strongly skewed toward high whorl counts, both when the whole samples are considered and when adult shells are excluded. Adult shells in these samples have 5.7 or more whorls; a 5.6-whorl adult was captured in October 1980. There is extensive overlap between adult and juvenile shells in the range of 5.7 whorls and above.

Probability paper analysis (HARDING, 1949) of juvenile shells in the May and October samples does not clearly resolve any separate size classes, probably owing to small sample size. With the assumption of equal rates of mortality and immigration-emigration for adults as for juveniles, and no anomalous years intervening, the data in Figure 3 imply at least as many year-classes of adults present as there are of juveniles. There may well be more; adult *Cepaea* age-classes for up to 5 yr after lip reflection have been detected (WILLIAMSON, 1979), and 10-yr-old *Helix pomatia* are probably not uncommon in natural populations (POLLARD *et al.,* 1977). VAN DER LAAN (1971) reported 6–10-yr longevity in *Helminthoglypta stiversiana.* SOLEM & CHRISTENSEN (1984) reported camaenid species with >8-yr longevity, and more than five year-classes of adults in a population.

Two autumn and six spring captures were in the process of secreting a reflected lip. If maturation and lip reflection coincide in *Monadenia setosa,* the onset of reproductive maturity is not tied to one season. Early summer reproductive activity has been recorded for the species (ROTH & ENG, 1980). It is not known whether individuals forming reflected lips in May mate and lay eggs the following June and July, although this seems plausible. Perhaps individuals forming reflected lips in October are capable of mating and oviposition that autumn and winter. A scattered (or bimodal?) timing of reproduction might be strategic in a region like the Klamaths where the duration and severity of seasons are varied and unpredictable. Alternatively, individuals forming reflected lips in the autumn may not become reproductive until the following spring.

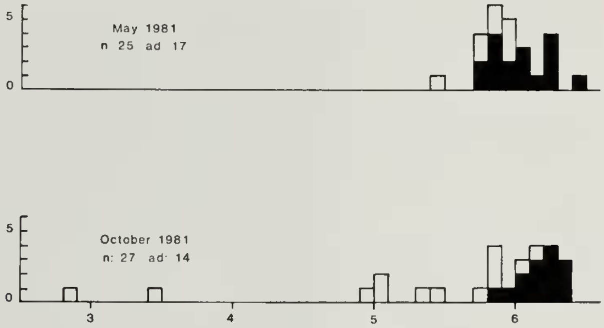


Figure 3

Number of individuals (ordinate) and whorl number (abscissa) in May and October 1981 samples. Adults (ad) indicated by solid bars.

Two individuals added reflected lips between the times of first and subsequent capture. Snail No. 3 had no reflected lip on 25 October 1980, but had begun to secrete one on 25 May 1981; whorl number was 5.8 on both occasions. Snail No. 30 had no reflected lip on 8 May 1981 but had one on 2 October 1981, adding 0.2 whorl in the interval. Snail No. 7 had 5.5 whorls on 25 October 1980, and 5.7 whorls on 2 October 1981, with no reflected lip added. Snails Nos. 43 and 44 are recorded as having the last quarter-inch of whorl clean on 27 May 1981, implying fresh growth, but nothing more than relative timing can be inferred.

These very limited size-frequency and growth data shed little light on population age structure. The paucity of small individuals (fewer than five whorls) suggests three possible interpretations: (1) they are present at the site but not effectively detected by our search method; (2) little recruitment by reproduction has taken place recently at the study site; or (3) individuals pass through the small size range very quickly, after which growth slows to more nearly the observed values.

The earlier study of *Monadenia setosa* (ROTH & ENG, 1980) indicated differences in site selection by juveniles and adults; the present study did not entirely corroborate those results (see below, "Substratum, location, and mobility"). But except for noting the possibility that, merely by being smaller, the young individuals were more easily overlooked, there is no way to judge the correctness of the first interpretation. The second interpretation, low recruitment, may be supported by the fact that the 2 yr preceding the beginning of this study were unusually dry. Heavy egg and (or) juvenile mortality, or reduced mating may have occurred. In *Helminthoglypta stiversiana,* copulation rate and egg production are correlated with rainfall (VAN DER LAAN, 1980).

Taken as average, the observed growth rates would imply an interval of 9 to 18 yr from hatching to maximum size. We strongly suspect that earlier growth is more rapid. Terrarium-raised *Monadenia fidelis beryllica* attained

Figure 4

Radular scrapings of *Monadenia setosa* on lichen on alder trunk (arrows).

maturity in 5 yr (records in California Academy of Sciences). The time to maturity is 1-3 yr in *Cepaea hortensis* (WOLDA, 1970; WILLIAMSON, 1979), 6.9 yr in *Achatinella mustelina* (HADFIELD & MOUNTAIN, 1980), 3-6 yr in *Caracolus carocollus* (HEATWOLE & HEATWOLE, 1978), and 3.0-3.75 yr in *Helminthoglypta stiversiana* (VAN DER LAAN, 1971). Some Australian camaenids become functional males after 2 yr (SOLEM & CHRISTENSEN, 1984). Ontogenetic variation in growth rate is a recognized phenomenon in pulmonate mollusks, sometimes related to the state of development of the gonad (WILBUR & OWEN, 1964). HADFIELD & MOUNTAIN (1980) found a relatively constant rate of growth in the Hawaiian tree snail *Achatinella mustelina* over a size range of about 6 to 18 mm length. The factors influencing growth pattern may differ between tropical and temperate environments.

Substratum, location, and mobility: Of 92 captures at the study site for which substrata were recorded, 30 were on the soil or leafmold of the ground itself. Nineteen were on the bark of alders from 0.25 to 7 m above the ground, 29 were on other objects, either stalks or twigs (14), logs or deadfalls (8), or rocks (7); four were in rockpiles, four under objects on the ground, and three under the bark of standing deadwood. Three were recorded as "in leafmold," as opposed to crawling on top of it.

In the mixed evergreen forest east and upslope from the study site, snails were observed in douglas fir needles on loose soil, at the edge of a decaying log, in a cavity under a decayed stump, and in depressions in the ground.

Some feeding takes place on smooth trunks of alder. Six snails were observed to be rasping the bark, and many trunks showed extensive marks of radular scraping (Figure 4). In each case the food was one or more species of the mosaic of encrusting lichens. No snails or feeding tracks were seen on larger trunks with furrowed bark. Feeding was also observed on the ground, with the food items being the petiole of a violet, a dendritic lichen attached to a twig (two cases), and an unidentified stalk. Nearly all snails observed on alder trunks were either extended or crawling, even if not feeding.

Small snails, less than 10 mm in diameter, were found on the ground on moss (1), on bark under a deadfall (2), and about 2.5 mm deep in leafmold (1). Snails between 10 and 20 mm in diameter were found feeding on alder bark 1-2 m above the ground (2), or in a rockpile (1). ROTH & ENG (1980) indicated that the preferred habitat of juveniles under 9 mm in diameter was under the bark of standing deadwood, but our results indicate a broader range of site selection by small snails. The three specimens found under the bark of standing deadwood during this study were 29.7, 29.6, and 26.4 mm in diameter; the first two were adults, the third was immature.

Figure 2a plots the locations of individual *Monadenia setosa* on a typical search occasion, 8 May 1981. In Figure 2b, straight lines connect the locations of successive captures over the course of the study. This convention is not meant to suggest that this is all the movement these snails have undergone. Rather, it is a minimum estimate, because a snail could be recaptured near its original capture site after having ranged much farther away. The 3-wk sampling interval is too coarse to pick up variation in short-term movement (*cf.* experiments of COWIE, 1980); the observations do not, therefore, bear directly on the dispersive potential of the species but rather illustrate the tendency for individual snails to remain within a limited part of the total habitable zone available to them. In the course of a single night's wandering, an individual snail can (and probably often does) travel farther than the distance between captures many months apart. Snail No. 9, for instance, was closer on the night of 3 October 1981 to its original (October 1980) site of capture than to its position when found the preceding night.

Not surprisingly, the perennial stream Bidden Creek was not crossed by any snails in the course of the study. Perhaps more significantly, the semicircular low bench on the north side of the creek remained devoid of snails throughout the study, although apparently offering suitable habitat. This plus the pattern of captures and recaptures indicate that the snails are not uniformly dispersed through their environment and that their distribution at any one time reflects historical factors and, probably, the tendency for *Monadenia setosa* to occupy a narrow home range. Several species of snails and slugs restrict their activities to limited areas (Heatwole & Heatwole, 1978) or return to specific sites after periods of activity (Potts, 1975; Cook, 1979; Rollo & Wellington, 1981). Recapture tracks of snails Nos. 1, 6–9, and 13 show association over time with specific shelter sites such as clumps of trees or logs on the ground. Snail No. 5 may have changed its association from an alder clump at its first capture in April 1981 to a downed log 3–4 m southwest the following October. Snail No. 2 may have shifted from one alder clump to another between May and October 1981.

The pattern of movement seems explicable in terms of the behavior under experimental conditions of the snails and slugs investigated by Rollo & Wellington (1981). These workers found that slugs (*Ariolimax columbianus*) were capable of long-term homing to a shelter, probably by chemosensory means. Individual slugs tended to home to one of several available shelters, even when all shelters had been occupied by slugs of the same species. Homing is, therefore, probably more complex than simple response to odor.

Rollo & Wellington (1981:figure 2) detected a seasonal trend in sheltering behavior, apparently related to the severity of the microclimate. Hot, dry weather can kill exposed mollusks (although snails, with shells that can be sealed against desiccation, are less vulnerable than slugs), and there is more risk in wandering far from shelter when conditions tend toward dryness. The summer drop in the number of active snails observed at the study site probably reflects the same phenomenon in *Monadenia setosa*. Similarly, in open conifer-sclerophyll stands, where suitable shelter is sparse and of small extent, homing behavior that intensifies with dryness (up to a point where the "preferred" strategy is to seal down and wait) may be significant to survival.

Balanced against the homing proclivity must be a dispersal tendency, although at this point the tradeoff cannot be specified. As Rollo & Wellington (1981:255) note, "no habitat remains favourable indefinitely, and animals must be capable of abandoning those that deteriorate and discovering new favourable areas." In their study, slugs vacated shelters that became fouled by dead individuals, as well as those that became dry or partly flooded.

Less dispersal would be expected in stressed or marginal habitats (Potts, 1975). Occurring as it does on the east edge of the range of its subgenus, *Monadenia setosa* may encounter marginal conditions more often than, for example, *M. fidelis* populations in the heart of the range. Reduced dispersal under such conditions must intensify genetic isolation and probably in many cases contributes to differentiation and speciation as in *M. setosa* and *M. callipeplus.*

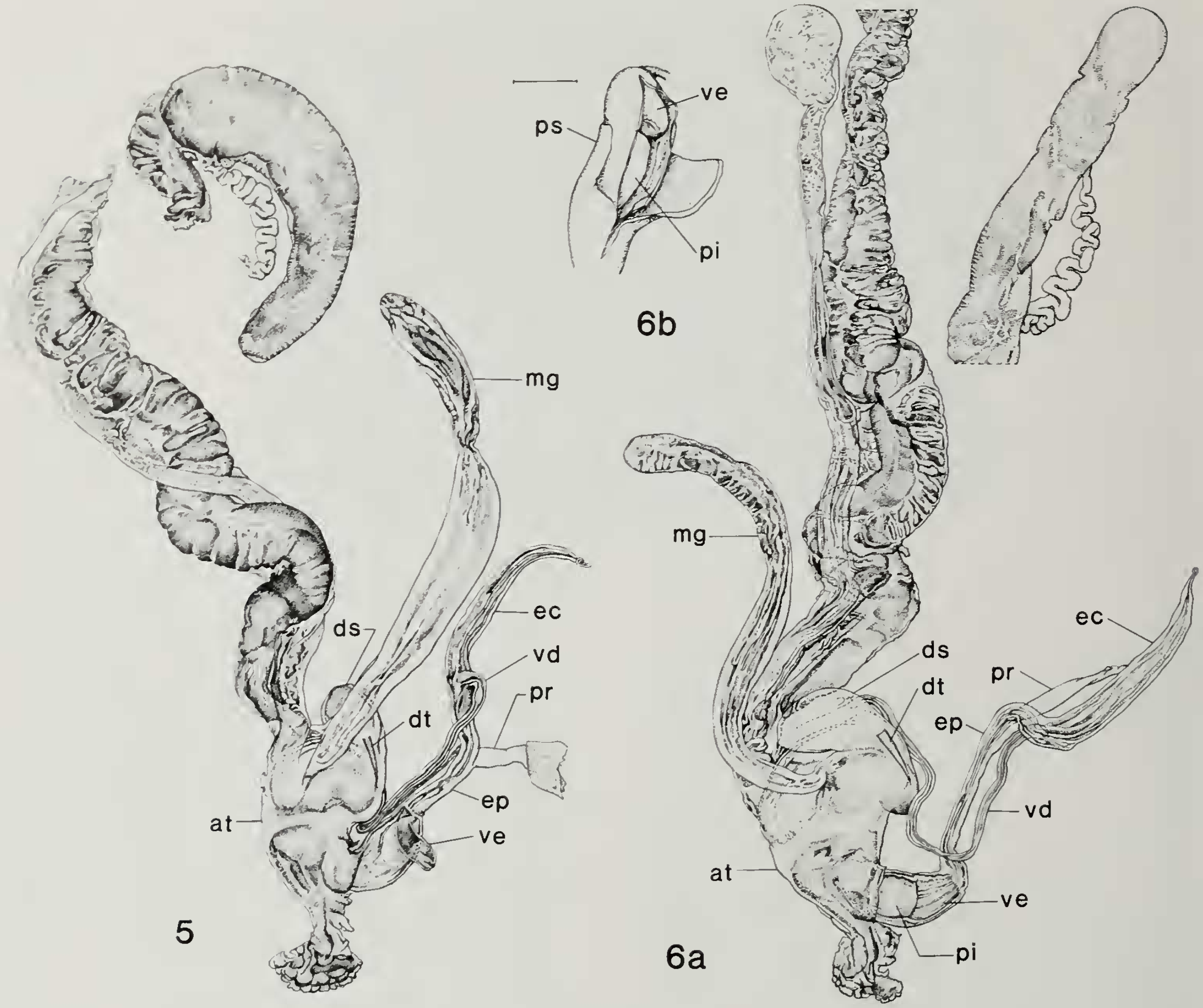
Predation: Evidence of two kinds of predation on *Monadenia setosa* was obtained. On 27 May 1981, snail No. 49 was found apparently freshly killed or stunned by a lampyrid beetle larva (*Ellychnia californica* Motschulsky; det. D. H. Kavanaugh, California Academy of Sciences). This species is commonly found inside dead snail shells in California and in the laboratory kills and devours *Helix aspersa* (Roth, personal observations). The snail was base-up on the ground, the animal withdrawn into its shell with just the tail tip showing, and the larva in the soil just beneath it. The snail showed no response to touch.

The upper limb of the aperture of many *Monadenia setosa* specimens shows small, frequently paired, indentations that suggest nipping by rodent teeth. Similarly indented growth lines occur on the body whorl of other shells. These must represent snails that escaped predation. Rodents may pick up the snails by the lip of the aperture, encounter some repugnatorial secretions of the mantle collar, and drop the snails. Roth & Eng (1980) previously reported probable rodent or shrew predation and insect parasitization.

COMPARISON of *MONADENIA SETOSA* AND *M. CALLIPEPLUS*

The original description and the few available museum specimens of *Monadenia* (*Monadenia*) *callipeplus* Berry, 1940, from Tompkins Creek (a tributary of the Scott River not far above the latter's confluence with the Klamath River) were similar enough to *M. setosa* to raise the question of whether it represented a remote occurrence of the same species.

On 27–28 April 1981, we found living *Monadenia callipeplus* sparingly among loose, dry black oak and canyon oak leaves and twigs on rocky ground, on the cliff at the south side of the mouth of Tompkins Creek. This locality is about 1.6 km downstream (east) from the original finding of *M. callipeplus* (according to Berry, 1940) but is connected with it by a continuous corridor of similar habitat, so there is no reason to doubt the identification. The type specimen of *M. callipeplus* was also taken among dry leaves and sticks. We also collected a sample of *Monadenia*



Explanation of Figures 5 and 6

Figure 5. Genitalia of *Monadenia callipeplus.*

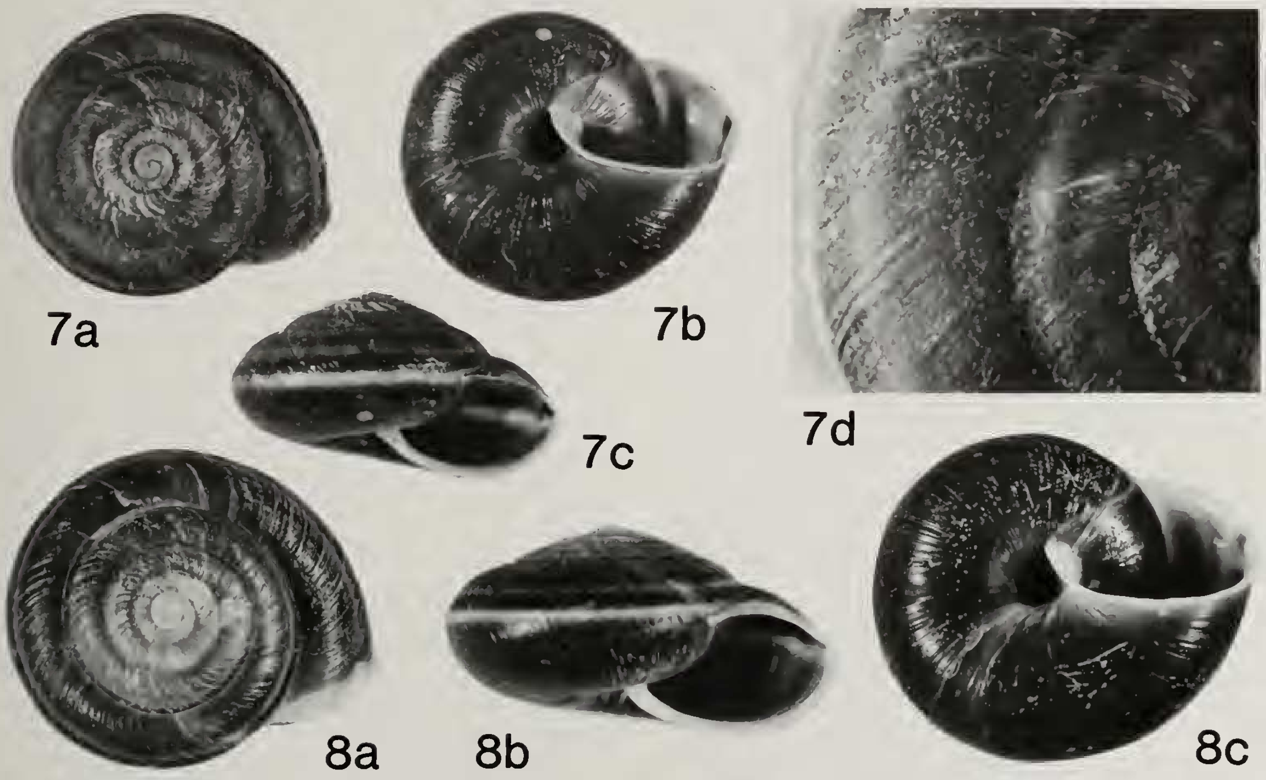
Figures 6a and b. Genitalia of *Monadenia scottiana.* Figure 6b. Detail of penis, opened to show pilaster and verge. at, atrium; ds, dart sac; dt, dart; ec, epiphallic caecum; ep, epiphallus; mg, mucus gland; pi, penial pilaster; pr, penial retractor muscle; ps, penial sheath; vd, vas deferens; ve, verge.

Scale bar = 2.2 mm for Figures 5 and 6a; 2.5 mm for Figure 6b.

(*Monadenia*) *scottiana* Berry, 1940, at Spring Flat campground on the Scott River, about 4.0 km south of Tompkins Creek. This proved useful in the interpretation of *M. callipeplus,* as described below.

The living animal of *Monadenia callipeplus* is slender and creamy buff with black shading on the dorsal tubercles. This is in contrast to the dark gray to black body of *M. setosa* with its brick-red to salmon colored tubercles. The mantle over the lung is buff with about 40% of its area covered by black maculations.

A stained whole mount of the genitalia was prepared by the method of Gregg (1959) (Figure 5). The basic structure of the genitalia is that of the subgenus *Monadenia* s.s. The flagellum (=epiphallic caecum, ec) is shorter than the penis plus the epiphallus, slightly curved but not spirally coiled except for a minute single coil at the distal end. The atrium (at) is small for the subgenus. The dart sac (ds) is proportionally large and contains a 2-mm, tusk-shaped dart (dt). The upper chamber of the penis is fig-shaped, wider below, with its cavity almost filled by a large, subcylindrical verge (ve) that is slightly wider at its free end; the free end is compressed with two labiate flaps, one on either side of the terminal meatus. The penial retractor muscle (pr) is broad and short; it inserts near



Explanation of Figures 7 and 8

Figure 7. Shell of *Monadenia callipeplus*. Figures 7a–c. Top, basal, and apertural views, ×1.5. Figure 7d. Detail of periostracal surface, ×7.5.

Figure 8. Shell of *Monadenia scottiana*. Figures 8a–c. Top, apertural, and basal views, ×1.5.

the middle of the epiphallus. The lumen of the vas deferens (vd) is dilated into a 1-mm ovate cavity about 0.75 mm from its insertion on the epiphallus. The lower, duct-like part of the mucus gland (mg) is stout; the lowest portion runs over the surface of the atrium to an insertion at the base of the dart sac.

Monadenia callipeplus is smaller than *M. setosa*. The shell (Figures 7a–d) is 22.5–25.3 mm in diameter in adults, compared to a mean of about 30 mm for *M. setosa*, although the smallest *M. setosa* examined (Loc. 2), at 23.7 and 24.1 mm, are smaller than the largest *M. callipeplus*. The umbilicus of *M. callipeplus* is proportionally somewhat larger (mean, 0.117× shell diameter); this difference is barely apparent without caliper measurement. The yellowish band below the periphery is brighter (*i.e.*, less obscured by periostracum) than in *M. setosa*. The periphery is subcarinate, the surface matte on the spire and base, and the periostracum bears short translucent setae and associated wrinkling, as described in detail by BERRY (1940).

These conchological distinctions by themselves would not be considered grounds for taxonomic separation of *Monadenia callipeplus* from *M. setosa*. The genital differences are more important and, by analogy with genital differences in other *Monadenia* species (ROTH, 1981), indicate that *M. callipeplus* and *M. setosa* are separate species. The verge of *M. callipeplus* differs from that of *M. setosa* (ROTH & ENG, 1980:figure 3A) in its terminal compression and presence of flaps. Because of its function in copulation, the verge is probably a good indicator of specific difference. In two sympatric *Monadenia* species in the Shasta Lake region, ROTH (1981) found that the main genital difference was in the shape of the verge. Other points of distinction include the large dart sac of *M. callipeplus*, its small atrium, and the proportionally longer flagellum.

The taxon described as *Monadenia fidelis scottiana* Berry, 1940, occurs at neighboring sites to *M. callipeplus* (BERRY, 1940) (Figures 8a–c). It is similar but has a shiny, dark brown periostracum, fine, discontinuous, incised spiral lines, and sparse, blunt papillation on the spire. No periostracal setae are present, but on the spire and base of some juvenile specimens there are fine, oblique, raised lines of periostracum, similar to those in *M. fidelis* from west of the range of *M. setosa.* BERRY (1940) mentioned specimens with papillation on the base as well. The genitalia (Figures 6a, b) show most of the typical characters of *Monadenia* s.s. The epiphallus (ep) is slender and the verge (ve) in the upper chamber of the penis is very large, obconic, with the free end larger in diameter than the base (Figure 6a). The basal chamber of the penis is deeply invaginated into the atrium. A single large pilaster (pi), with its distal end abutting the flat end of the verge, extends into the basal chamber on the side of the penis opposite the vagina. The penial retractor muscle (pr) inserts on the distal one-third of the epiphallus. The dart sac (ds) is large. On the wall of the atrium (at) below the dart sac there is a heavily staining, apparently glandular patch. The mucus gland (mg) is free from the atrium for most of its length, only the extreme lower portion being adnate. The atrium is not conspicuously small. These characters are constant in the two specimens dissected. They indicate that the taxon is distinct from *M. callipeplus* and from *M. fidelis* as well. It is accordingly raised here to species rank, *M. scottiana.*

Another species from the same general region is *Monadenia chaceana* Berry, 1940, of the Shasta River Canyon. ROTH (1981) mistakenly associated this species with *Monadenia* (*Shastelix*) *troglodytes* Hanna & Smith, 1933; but anatomical mounts made available by W. B. Miller show that *M. chaceana* is a member of *Monadenia* s.s. In two specimens from near the confluence of the Shasta and Klamath rivers, Siskiyou county (WBM 5172), the flagellum is about as long as the penis plus the epiphallus, tapering distally to a slender, subcylindrical tip. Both atrium and dart sac are smaller than in *M. scottiana*; the dart sac is shorter in proportion to the atrium. As in *M. scottiana* there is a heavily staining patch below the dart sac. The summit of the penis is markedly broader than the epiphallus. The verge in the upper penial chamber is convexly conical, and the meatus subterminal. Below the verge, the median wall of the chamber is thickened. The penial retractor muscle is slender and longer than the flagellum. The spermathecal duct is much more slender than in *M. scottiana,* in which it is somewhat cavernous for its entire length.

Monadenia callipeplus, M. scottiana, and *M. chaceana* are all similar in size and shape of the shell, but no intermediate populations are known. Zones of hybridization or intergradation, if they exist, must be very narrow. We interpret these three taxa as autochthonous (locally evolving, rather than immigrating) species, arising under conditions of isolation along the eastern edge of the range of *Monadenia* s.s. As one moves farther from the coast, mesic habitats become less extensive and more likely to be broken up into a series of habitat islands whose isolation persists for many generations. *Monadenia callipeplus* is, therefore, probably more closely related to its neighboring species *M. scottiana* and *M. chaceana* than it is to *M. setosa.* Because a transparent, unornamented periostracum is believed to be the ancestral condition in *Monadenia* (ROTH, 1981), periostracal setae must be separately evolved in *M. callipeplus* and *M. setosa* and not indicative of a direct patristic relationship.

The scenario presented here for the speciation of *Monadenia callipeplus, M. scottiana,* and *M. chaceana* probably applies also in the case of *M. setosa* (*cf.* ROTH & ENG, 1980:15). The narrow zone of apparent intergradation along the western margin of the range of *M. setosa* indicates that genetic isolation from *M. fidelis* is not complete.

MANAGEMENT IMPLICATIONS

This study revealed that there are a number of more or less discontinuous zones of riparian understory that support populations of *Monadenia setosa.* If the Bidden Creek monitoring site is taken as an example (and it may be more nearly an optimum), population densities of 0.11 snail/m^2 may exist in many of these zones. Lesser densities may be present on slopes of mixed evergreen forest away from the riparian corridors. In every case the presence of snails seems to depend on the availability of suitable microhabitat: physical shelter in which the animals can withstand seasonal climatic fluctuations.

The low rates of growth observed suggest that recovery from any population catastrophe would be slow. The tendency for snails to occupy a limited home range and to forage in specific areas indicates that repopulation from adjacent areas would be slow and subject to chance. It is quite possible that the population on the lower benches of Swede Creek, where the species was first collected (TALMADGE, 1952), then sampled by other biologists, has not yet recovered from such sampling. In consequence, the earlier field study (ROTH, 1978; ROTH & ENG, 1980) probably underestimated the abundance of the species as a whole, even for the part of the range then known.

The pattern of captures in the monitoring study shows that May and October are the months of greatest activity. Search at any other time of year is likely to underestimate numbers or lead to the conclusion that snails are absent from a site where they do in fact occur. Early morning and after dark are the best times to detect active snails. Discovery of either *Monadenia fidelis* or *M. churchi* at a site is circumstantial evidence that *M. setosa* does not occur there; these species have never been found microsympatrically.

The fortunes of *Monadenia setosa* are tied to the availability of mesic habitat. The shading, temperature- and humidity-regulating qualities of riparian woodland with its dense understory are crucial. Appropriate physical niches exist here and there in open stands of mixed conifer-sclerophyll forest but cannot be counted on to be as extensive, as stable, or capable of supporting large snail populations as the riparian corridors.

The question of vegetational succession can be viewed in the same terms. The critical factors are probably not the plant species per se but the related physical conditions: moisture retention, leafmold on the ground, shade, and temperature modulation. Any opening up of shading understory could be expected to favor *Monadenia churchi* and its associated species. Advanced stages of forest decadence favor *M. setosa* and its associated species because of increased availability of protective cover (as around and under deadfalls and brushpiles) and enhanced slope stability.

Before targeting a particular area of understory for protection and excluding others, a careful search under optimal seasonal conditions should be made to determine the presence and deployment of viable *Monadenia setosa* populations. In general, the conclusions of the 1978 study regarding substrate, shelter, and forest decadence conditions still hold, although the present study indicates (1) that juvenile dependence on standing deadwood was overestimated and (2) that there is limited occurrence outside of riparian corridors.

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APPENDIX: LOCALITIES

Localities yielding land mollusks in the course of this study are listed below; they are characterized as either (*A*) within the zone of dense deciduous understory or (*B*) in stands of open growth. *Monadenia setosa* was found at localities marked by an asterisk (*). Localities with range west (W) are located with reference to Mount Diablo Base and Meridian; localities with range east (E) are located with reference to Humboldt Base and Meridian.

1. Springs by Forest Service Road 5N16, E of Barnum Ridge, SE¼ SE¼ sec. 7, T. 5 N, R. 8 E (*B*). ***2.** Limestone talus slope W of Forest Service Road 5N16, SW¼ sec. 32, T. 6 N, R. 8 E (*B*). ***3.** Drainage of Swede Creek from seep areas at head to crossing of Big Mountain Road, NE¼ sec. 1 to NW¼ sec. 13, T. 5 N, R. 7 E (*A*). ***4.** Bidden Creek, north of Forest Service Road 4N47, SW¼ SE¼ sec. 19, T. 4 N, R. 8 E (*A*). **5.** Unnamed creek tributary to McDonald Creek at Forest Service Road 60 S of Burnt Ranch, NW¼ sec. 22, T. 5 N, R. 6 E (*A*). ***6.** Unnamed Creek along Forest Service Road 4N16 at first switchback S of Big Bar, SE¼ SW¼ sec. 6, T. 4 N, R. 8 E (*A*). **7.** Mud Spring, NE¼ NW¼ sec. 21, T. 4 N, R. 8 E (*B*). **8.** Near head of Price Creek at Forest Service Road 4N16, ctr. sec. 28, T. 33 N, R. 12 W (*A*). **9.** Unnamed creek tributary to Packers Creek at Forest Service Road 4N16, SW¼ NE¼ sec. 36, T. 33 N, R. 12 W (*A*). **10.** Roadside spring creek on Calif. Hwy. 3 NE of Hayfork Summit, ctr. sec. 21, T. 32 N, R. 10 W (*B*). ***11.** Big Creek, along Big Creek Road 0.25 mi N of intersection with Forest Service Road 4N16, N ctr. sec. 6, T. 32 N, R. 11 W (*A*). ***12.** Limestone Creek 0.125 mi upstream from confluence with Big Creek, SE¼ NE¼ sec. 31, T. 33 N, R. 11 W (*A*). **13.** Small stream by road along E branch of N Fork Trinity River, SW¼ SW¼ sec. 16, T. 34 N, R. 11 W (*A*). **14.** Manzanita Creek, N and S of Calif. Hwy. 299 bridge, NE¼ NE¼ sec. 5, T. 33 N, R. 12 W (*A*). **15.** E branch of N Fork Trinity River at road crossing, SE¼ SE¼ sec. 5, T. 34 N, R. 11 W (*A*). **16.** Near head of Big Bar Creek at Forest Service Road 4N16, NW cor. SE¼ sec. 27, T. 33 N, R. 12 W (*A*). **17.** Don Juan Creek, for 0.25 mi N of Calif. Hwy. 299, SW¼ sec. 20, T. 5 N, R. 7 E (*A*). **18.** E bank Cedar Flat Creek, SE¼ SW¼ sec. 19, T. 5 N, R. 7 E (*A*). ***19.** Banks of Swede Creek between Calif. Hwy. 299 and Olasson Ranch, NE¼ sec. 23, T. 5 N, R. 7 E (*A*) [type locality of *M. setosa*]. **20.** Limestone rockslide N of Calif. Hwy. 299, 0.4 road mi E of Del Loma, NE¼ SE¼ sec. 25, T. 5 N, R. 7 E (*B*). **21.** Upper and lower riparian benches, E side Canyon Creek, NE¼ NE¼ sec. 30, T. 35 N, R. 10 W (*A*). **22.** Natural Bridge, SE¼ sec. 33, T. 31 N, R. 11 W (*A*). **23.** 3.9 mi W of Trinity River bridge at Big Bar, rockslides N of Calif. Hwy. 299 (*B*). **24.** Limestone outcrop near mouth of Manzanita Creek at Calif. Hwy. 299, NE¼ NE¼ sec. 5, T. 33 N, R. 12 W (*B*). **25.** Hawkins Creek drainage along Forest Service Road 7N01, NW¼ NW¼ sec. 22, T. 6 N, R. 6 E (*B*). **26.** Soldier Creek Loop, NE¼ SW¼ sec. 27, T. 33 N, R. 11 W (*B*). ***27.** S side Trinity River 0.125 mi E of confluence of Price Creek, SW¼ NE¼ sec. 5, T. 33 N, R. 12 W (*A*). **28.** New River drainage, NW¼ NE¼ sec. 13, T. 6 N, R. 6 E (*A*). ***29.** Hill slope E of Bidden Creek N of Forest Service Road 4N47, SW¼ SE¼ sec. 19, T. 4 N, R. 8 E (*B*). ***30.** W bank Big French Creek, first large terrace N of Calif. Hwy. 299, NE¼ SW¼ sec. 20, T. 5 N, R. 8 E (*A*). **31.** Bell Creek, SW¼ SE¼ sec. 12, T. 6 N, R. 6 E (*A*). **32.** Madden Creek, up trail 300 yd from washed out bridge, ctr. SW¼ sec. 21, T. 6 N, R. 5 E (*A*). **33.** Hawkins Creek above confluence with unnamed tributary stream, NW¼ SE¼ sec. 9, T. 6 N, R. 6 E (*A*). **34.** Unnamed creek tributary to Eltapom Creek, ctr. NW¼ sec. 36, T. 4 N, R. 6 E (*A*). **35.** South-facing pebbly talus slope E of mouth of Little Swede Creek, SW¼ NW¼ sec. 24, T. 5 N, R. 7 E (*B*). ***36.** Little Swede Creek, SW¼ NW¼ sec. 24, T. 5 N, R. 7 E (*A*). **37.** Hennessy Ridge Road, 2.3 mi up from start of Forest Service Road 6N12, ctr. SW¼ sec. 30, T. 6 N, R. 6 E (*A*). **38.** Hillside W of Swede Creek between Calif. Hwy. 299 and Olasson Ranch, NW¼ NE¼ sec. 23, T. 5 N, R. 7 E (*B*).